On the Ontogeny of Display Behaviour in the Black-Headed Gull

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ON THE ONTOGENY OF DISPLAY BEHAVIOUR IN THE BLACK-HEADED GULL:

II. CAUSAL LINKS BETWEEN THE DEVELOPMENT OF AGGRESSION, FEAR AND DISPLAY BEHAVIOUR: EMANCIPATION RECONSIDERED

by

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(With 13 Figures)
(Acc. 15-X-1988)

1. Introduction

1.1. The problem.

In part I of a study on the ontogeny of display behaviour in the black-headed gull (*Larus ridibundus*) (GROOTHUIS, 1989), it was found that the displays gradually reach their adult form, through a series of "precursors". Incomplete postures are gradually replaced by more complete ones, through addition or change of separate form elements (GROOTHUIS, 1989, Fig. 1). Several possible mechanisms for the morphogenesis of display behaviour were discussed. The study presented here is especially focused on the role of internal factors controlling agonistic behaviour in the ontogeny of displays.

KRUIJT (1964) has made one of the most thorough studies of the ontogeny of agonistic behaviour. He reported several changes in agonistic behaviour in the course of ontogeny:

1) This study was largely inspired by Gerard BAERENDS, who took the initiative for the studies on communication behaviour in gulls, and by Jaap KRUIJT, who's study on the ontogeny of communication behaviour in the Burmese red junglefowl was a fruitful basis for the study presented here. I am greatly indebted to both of them for their continuous support and inspiration. This work has also greatly benefitted from discussions with Johan van RHIJN, Jan VEEN, Carel ten CATE and Nance VODEGEL. The former two also assisted in solving all kinds of practical problems during the observation periods. Leo van MULEKOM assisted in collecting and analyzing the data, presented in Figs 10 and 11. The "Rijksdienst voor de IJsselmeerpolders" kindly gave permission to work in their sanctuary. Raising the young gulls in the laboratory would have been much more difficult without the help of the animal care takers, especially Sjoerd VEENSTRA, Bram de HAAN, Gerard BAKKER and Auke MEINEMA.

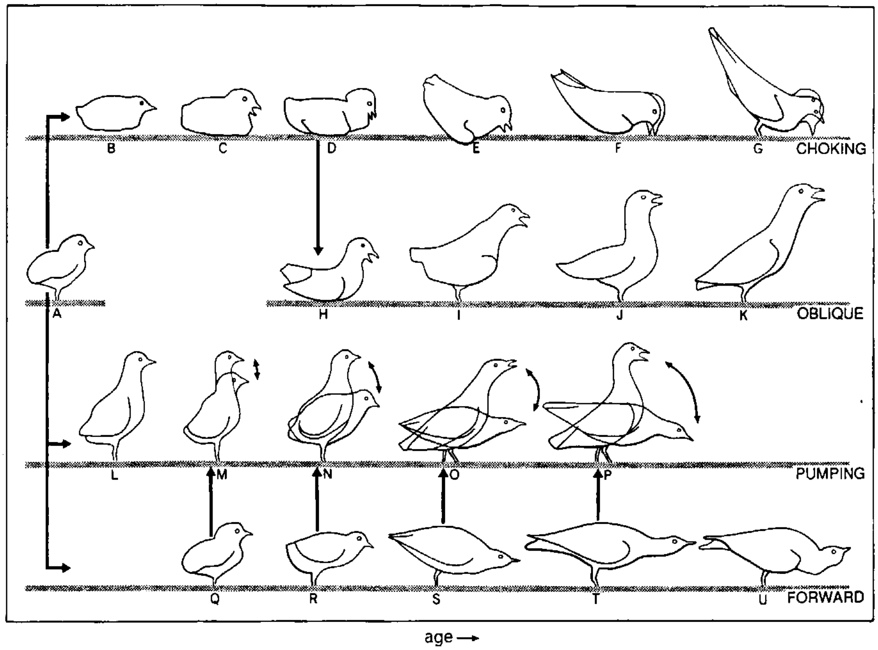

Fig. 1. Development of the form of the four main displays in young black-headed gulls. (After GROOTHUIS, 1989).

1. A gradual development of aggressive and fear behaviour early in ontogeny;
2. A decrease in frequency of overt aggression, overt fear, and of the alternation between these two, later in ontogeny;
3. A gradual increase in display frequency;
4. An increase in frequency of longer lasting and more complex interactions. He hypothesized that in the course of ontogeny motivational factors for aggressive and fear behaviour gradually increase in strength, and increasingly interact with each other, leading to less overt aggression and fear, and to more frequently performed agonistic display. Inspired by his interpretation, GROOTHUIS (1989) raised young gulls in a situation lacking the normal context for agonistic behaviour, in an exploratory attempt to manipulate the normal course of display development. These birds showed hardly aggressive behaviour and a retardation in development of their display was found. This suggests that the development of display is related to the development of aggressive and fear behaviour.

A relationship between internal factors for aggression and fear on the one hand and display behaviour on the other was for the first time explicitly postulated in the so called "conflict-hypothesis" (TINBERGEN, 1952; for a review see BAERENDS, 1975). This hypothesis assumes that displays originate from simultaneous activation of different behavioural systems — in particular those controlling aggression and fear behaviour — incompatible with each other in their expression when strongly aroused. In line with this hypothesis, in the form of many display postures or calls elements of both attack and escape behaviour have been found (KRUIJT, 1964; LEYHAUSEN, 1956; TINBERGEN, 1959; VEEN, 1987). Although the conflict-hypothesis was primarily meant to explain the evolutionary origin of displays, for testing it arguments derived from the proximate causation of displays have been amply used, in particular the temporal relationship of attack and escape with display behaviour (*e.g.* for gull displays: MANLEY, 1960; MOYNIHAN, 1955). Consequently it is often assumed that the displays are presently still under the influence of internal factors for aggressive and fear behaviour, and that the motivational state of the animal is reflected in its display.

However, game-theoretical models predict that during agonistic interactions an animal should not give away reliable information about its fighting strategy, such a how long it is willing to display, or its intention to attack (MAYNARD SMITH, 1982). Based on this functional point of view (CARYL (1979) and others argued that displays performed during agonistic encounters are unlikely to be under the control of an internal factor controlling aggressive behaviour. Otherwise displays would reflect the motivational state of the animal and consequently give away reliable information about its fighting strategy. Inspired by these theoretical consideration, CARYL (1979) re-analysed part of the data on display and subsequent attack and escape in birds, earlier presented as support for the conflict hypothesis. He concluded that in the case of these data display performance does not allow a reliable prediction of subsequent attack. This is in line with the predictions of the game-theoretical models, and it has been presented as an important argument to reject the possibility that displays are presently motivated by a tendency to attack and to flee.

It should however be realized, that the game-theoretical models involved were crude simplifications of the interactions occurring between real animals in the field, and that their predictions bear heavily on assumptions, made explicitly or implicitly, about the situation of the conflict. For example, VAN RHIJN & VODEGEL (1980) found that transmission of reliable information about the intention to attack can be an evolutionary stable strategy when the birds know each other individually. Furthermore, the relation between conceptions used in the game-theoretical approach and those used in ethology is not clear. For example, it is questionable whether the term "intention", as originally used by Maynard Smith, may be translated by the concept of "motivation". For a more detailed discussion on this subject, see VAN RHIJN (1980); HINDE (1981); ARCHER (1988). So, although results of these models can be an important guide for further ethological studies they can never give the final answer to the problem of motivation of displays in real animals.

Inspired by the studies of MAYNARD SMITH ethologists realized that the methods used so far for the analysis of communication behaviour had often been rather crude. For example, the reactions of the opponent to the display performed by the actor can have an important effect on the attack probability of the latter (BOSSEMA & BURGLER, 1980), but these reactions have rarely been taken into account. Moreover, experimental testing of the interpretations on the causation of displays had not occurred. Consequently there still is a shortage of thorough quantitative studies on the causal organization of agonistic behaviour. The few studies which have been done indicate that, at least in some cases, internal variables controlling overt aggressive and fear behaviour, determine display behaviour, depending on their activation both in an absolute and in a relative sense (BLURTON JONES, 1968; VODEGEL, 1978; for reviews see BAERENDS, 1975 and HUNTINGFORD & TURNER, 1987). Furthermore, computer simulations of agonistic behaviour of individuals in contests between conspecifics, on the basis of interaction of two independent "motivational" factors, produced good mimics of the observed agonistic behaviour in real animals (VODEGEL, 1978; MAYNARD SMITH & RIECHERT, 1984). Therefore, and because of the importance to understand the causal basis for agonistic behaviour, the hypothesis that internal factors for aggression and fear are involved in the control of display behaviour seems worthwhile to be studied further.

1.2. Methods of approach.

An important starting point of this study is the hypothesis that the following principles hold for the organization of behaviour:

1. The groupwise appearance of different, often (but not necessarily always) functionally related motor patterns is due to one or more internal common causal factor(s):

2. Several of these factors are often simultaneously aroused;
3. These factors often compete with each other for their expression in the final motor output (*e.g.* BAERENDS, 1975).
Furthermore, several authors are of the opinion that the structure of the causal organization of behaviour is gradually built up during ontogeny (FENTRESS & MCLEOD, 1987; KRUIJT, 1964; PLOOY, 1980). Consequently, it is conceivable that a relation between aggression and display in adults is hard to establish, not because this relation is not existing, but because the increasing complexity of agonistic behaviour masks the role of internal factors controlling aggression and fear in the causation of displays in adults. These considerations speak for an approach in which the organization of aggressive, fear and display behaviour is studied already from the beginning of ontogeny.

In the study presented here, it was investigated whether changes in form and frequency of the displays in the course of ontogeny of black-headed gulls could be explained by changes in aggressive and fear behaviour. Preliminary field observations revealed that chicks from the age of two weeks on are already involved in territorial defence. Young of the same nest frequently have agonistic interactions with young and adult birds of closely neighbouring nests. However, these interactions were difficult to record. Moreover, data on ontogenetic changes in agonistic behaviour were difficult to obtain under field conditions, because the young leave the colony at the age of 5-7 weeks. For these reasons, the observations and experiments were done at the laboratory. Chicks were raised in large groups of birds of the same age. In these conditions, young gulls form small subgroups of 2-4 individuals within a large group, each defending part of the cage and, during bathing, the water pool, against other subgroups. This resembles the above mentioned field situation.

Changes in agonistic behaviour in the course of ontogeny were studied in two ways:
1. Agonistic behaviour of the young was tested weekly during their first 9 weeks of age. This was done by confronting them with a standard stimulus object, simulating an adult intruder on the territory. In this way it was tried to exclude possible effects of (changes in) the behaviour of the opponent on changes in the behaviour of the subjects.
2. Analyses of mutual interactions amoung the young. This was done because older gulls hardly responded with agonistic behaviour in standard stimulus tests.

Data were obtained concerning frequency, form, orientation and temporal relations of overt aggression, overt fear and display postures. In addition, data concerning locomotory behaviour were collected in the expectation that the temporal associations of locomotory categories (*e.g.* approach and withdrawal) and the occurrence of displays during these categories would give important information about the organization of agonistic behaviour.

The presentation of the results of this study (section 3) is structured in the following order:

Section 3a deals with the results of the standard stimulus experiments, carried out in groups of young gulls.

— First, the development of overt aggressive and overt fear behaviour is described (part 3a.1 a and b), as well as changes in ontogeny in the relation between aggression and fear (3a.2).

— Second, the development of three display postures is described (3a.3).

— Third, the development of display is related to changes in ontogeny of aggressive and fear behaviour (3a.4).

— Finally, the influence of an internal factor for aggression on display behaviour is tested experimentally by manipulating the former by means of an experiment in which young gulls were treated with testosterone (3a.5).

In section 3b agonistic behaviour of young and adult gulls is compared, mainly on the basis of data obtained from mutual interactions. Changes in the relation between aggression, fear and display are described.

— To this end, data concerning a shift in frequency of overt aggressive and fear behaviour to display behaviour, and the temporal relation between display and aggression are presented in 3b.1.

— Because adult gulls hardly perform overt aggression and fear behaviour, changes in agonistic behaviour with increasing age are analyzed in part 3b.2, on the basis of the following data: changes in the timing of displays in relation to the locomotion of the birds themselves and to the behaviour of the opponents; changes in the context in which the display are performed.

The discussion (section 4) concentrates on two main points:

— The development in frequency and form of each single display in relation to the development of motivational factors for aggressive and fear behaviour.

— A change in motivation of displays occurring in older gulls after the displays have been developed and their forms have become fixed.

2. Material and techniques

2.1. Raising conditions.

a. *Large groups.*

Most of the data presented in this paper are obtained from the behaviour of gulls, raised in large groups. Young black-headed gull chicks were collected in the field at an age of approximately 5 days. Until the age of 4 weeks, they were raised in large groups of 17 individuals, in indoor cages of 3.5 × 1 m, containing several hiding shelters, and food and water containers. Thereafter most of these birds were placed in groups of 7-9 birds in outdoor aviaries of 3.6 × 1.8 m, containing one bathing pool. Some of the birds were placed in larger aviaries (at least 50 m^2), containing at least 5 adult birds which had been raised in approximately the same way. All birds were mainly fed with pellets produced for mink or trout farms, mixed with water for young birds. Water of the bathing pools was refreshed at least 3 times a week.

b. *Semi-natural condition.*

To control for the artificial raising condition described above, it was tried to have young raised by adult gulls. Several breeding pairs were kept in a large aviary; in case they lost their own chicks they were supplied with hatching eggs or young of less than 1 week of age. The behaviour of parents and chicks was observed for several hours a week. For more details see GROOTHUIS, 1989a.

c. *Chicks, treated with testosterone.*

Eggs were collected in the field and hatched in the laboratory. The chicks were raised in 3 small groups of 4-5 conspecifics in indoor cages of approximately 1.5 × 0.7 m. In every group 1 or 2 individuals were implanted with a 25 mg pellet of testosterone proprionate, subcutaneously in the neck region, at the age of 5 days.

2.2. Standard stimulus experiments.

The development of agonistic behaviour of young gulls, raised in large groups and of the chicks, treated with testosterone, was studied by means of standard stimulus experiments. Young raised in large groups were tested with a stuffed adult black-headed gull at least once a week during their first 7 weeks of age. The stuffed bird was mounted on the end of a long stick, and moved slowly through the whole cage. During the time the young responded with display or aggression the model was held more or less stationary, and slightly shaken.

Because older young are easily frightened by models, a living adult conspecific was used from the time the young were 5 weeks old until they reached the age of 10 weeks. Thereafter they hardly responded to the stimulus bird anymore. The stimulus bird whose wings were clipped, behaved rather "neutrally" during the experiments, showing neither aggressive behaviour nor display. All standard stimulus experiments were filmed and analyzed by means of video equipment.

The chicks treated with testosterone were tested twice during their first 2 weeks of age with the stuffed adult black-headed gull.

2.3. Classification of the behaviour observed.

a. *Aggressive behaviour and other pecking movements.*

Overt aggressive behaviour in gulls consists of aggressive pecks, and was measured by form and frequency of the latter. Three types of pecking were distinguished:

1. Aggressive pecks. They consist of a rapid forceful movement of head and bill towards the stimulus which, as a consequence, may receive considerable damage.

2. Incomplete aggressive pecks. Aggressive pecks were classified as incomplete when the movement was stopped before the bill reached the object. In the analysis of overt aggression these pecks were lumped with complete pecks, unless it is explicitly mentioned that this was not done.
3. Bill pecks. These consist of pecks normally directed towards the parents while begging for food. In chicks of more than one week old they can be distinguished from aggressive pecks by the very gentle character of the movement which is always directed at bill or throat. Chicks less than one week old often put considerable force in bill pecks. But such pecks are distinguishable from aggressive pecks by the following properties: a snapping bill movement; grasping the bill of the stimulus object; accompanying begging sounds (the Pee-call, see GROOTHUIS, 1989, and also HAILMAN, 1967).

In superposition upon this classification, the form of all three types of pecking was classified in three types of movements:
1. Movements, in which the head was clearly extended above the body (these erect pecking movements concerned almost exclusively aggressive pecks).
2. Movement, starting from a resting posture, in which the head was held more or less upon the body, and in which the neck was not extended in upward direction during the peck itself.
3. Forward-like movements in which the head moved in front of the body (mostly bill pecks in older young).

b. *Fear behaviour.*

Two forms of fear behaviour were distinguished:
1. Withdrawal: a movement away from the stimulus, often running, but also walking or turning away for more than 90 degrees.
2. Sitting: at least part of the body touching the ground. Sitting often immediately followed withdrawal, and was mostly performed in a crouched position while hiding in one of the artificial shelters or between other chicks.

c. *Locomotory behaviour.*

Five categories of locomotory behaviour were distinguished:
1. Approach: the bird moved to the stimulus, either by running, walking or turning over more than 90 degrees.
2. Withdrawal: see above.
3. Sitting: see above.
4. Standing still.
5. Stopping: an, often sudden, break in the movement towards or away from the stimulus, after which the bird stood still. When a bird changed its posture during stopping, stopping was recorded as changing into standing still.

d. *Display behaviour.*

The display repertoire of adult black-headed gulls consists of four main displays: the oblique, choking, the forward and the upright (MOYNIHAN, 1955). Incomplete or complete forms of the first three displays were frequently seen in young gulls, while upright-like postures were almost completely absent. Besides these displays, young gulls often perform the begging display, which consists of a rapid pumping movement of the neck and head, while in every downward beat the begging call is uttered. All incomplete- or complete forms of display performed by the young gulls were classified into one of the four main categories distinguished by GROOTHUIS (1989a):
— All erect postures, performed with long-call like vocalizations, were scored as oblique-like postures.

— Postures in which the neck was held less than 45 degrees above the horizontal, and in which the bill pointed downwards, were classified as choking-like postures.
— Postures in which the head was held in front of the body were distinguished as forward-like postures.
— All pumping movements were classified as pumping.

The only other posture which was classified separately was the alert posture. It consists of an erect posture, in which the neck is thinned and considerably stretched vertically upwards. In contrast with the oblique-like posture, the alert posture is often performed silently or together with the alarm- or rattle-call.

3. Results

3a. Development of agonistic behaviour in young gulls in response to standard stimulus objects.

3a.1. Development of aggressive and fear behaviour.

a. *Aggression: frequency, form and orientation of pecking behaviour.*

The average frequency during the ontogeny of pecking movements in the standard stimulus experiments in the large groups is given in Fig. 2a. The scores obtained from the model experiments and those obtained with a live bird are plotted separately. Initially, bill pecking was very high, in accordance with the finding that in young chicks this begging behaviour is easily evoked by bill shaped objects (HAILMAN, 1967). It decreased considerably during the first week. Aggressive pecks only appeared at the end of that week, by the time normally raised chicks start to recognize their parents and siblings individually (VAN RHIJN & GROOTHUIS, 1985). These pecks gradually increased in frequency until the age of 23 days; the mean number of pecks per bout rising from 1 to 1.8. By that time, the young behaved very aggressively and had prolonged fights with members of other subgroups and with the model. This resulted in considerable damage to the model as well as to other young. Several individuals had callow heads.

After the age of four weeks, aggression to the model decreased, but to the living gull it remained very high. After five weeks, by the time the young fledged, the frequency of aggressive behaviour dropped to zero. Between the 5th and 9th week, the percentage of incomplete aggressive pecks strongly increased. The decrease in aggression is unlikely to be due to habituation to the standard stimulus, since birds of more than 7 weeks of age, when confronted for the first time with the model or the living bird, hardly showed any aggression.

To check whether the changes in frequency of aggression in the course of ontogeny were artefacts of the experimental raising condition, aggressive behaviour was also studied in four young in the semi-natural

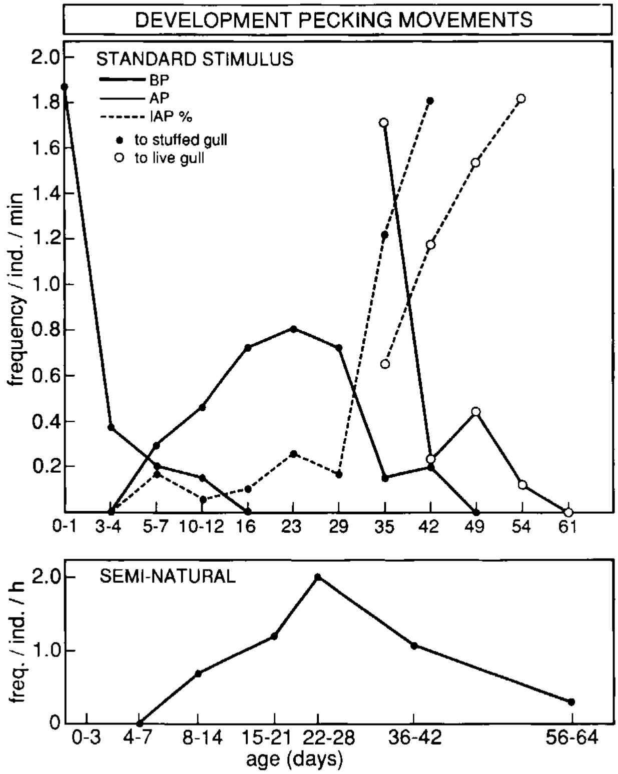

Fig. 2. a: Average frequency per individual per min of pecking movements in standard stimulus experiments during ontogeny. Data are given both for experiments in which a stuffed black-headed gull was used and in which a live one was used. BP = bill pecking. AP = aggressive pecking. IAP% = percentage of aggressive pecking which was classified as intentions to aggressive pecking. b: Mean frequency per individual per hour during ontogeny of aggressive pecks in a semi-natural context (see text).

situation. The average frequency of aggressive pecks, they directed to other young as well as to adult intruders on the territory is depicted in Fig. 2b for 6 age classes. If follows almost the same course as in Fig. 2a, suggesting that the results obtained in the experiments are representative for the behavioural development in the field.

Not only the frequency, but also the form of pecking behaviour changed with age. The frequency of different forms of aggressive pecks and of bill pecking is given in Fig. 3. Because in the experiments bill pecking was hardly performed by older young, these data were collected in the semi-natural situation. In very young chicks (0-3 days), none of

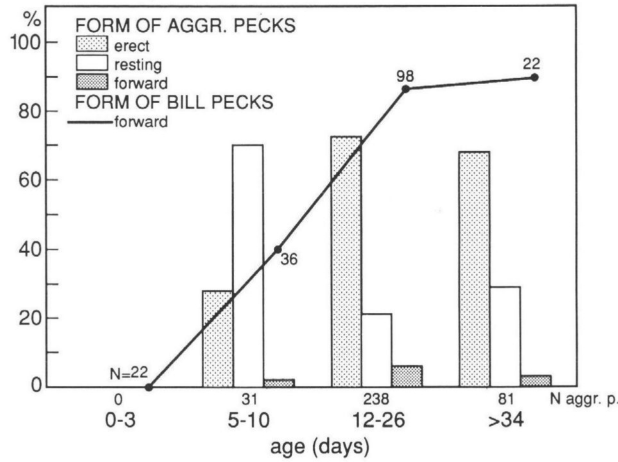

Fig. 3. The relative frequency of different forms of aggressive-pecks (bars) and of bill-pecks (line), performed by young gulls of four age-classes, in the semi-natural condition.

the bill pecks consisted of forward-like pecks; in fact almost all begging-pecks were carried out from resting postures. The first aggressive pecks, seen in chicks of 5-10 days old, also mainly consisted of this kind of movements. In older birds, aggressive and bill pecking became increasingly different in form. Bill pecking was more and more performed in a forward-like movement (without extended carpal joints and followed by a gentle peck with small amplitude). In contrast, aggressive pecks were increasingly carried out in an erect position, often performed with raised carpal joints or wings, and followed by a forceful downward peck. The increase in erect forms of aggressive pecking was highly significant ($\chi^2 = 24.49$, $p < 0.001$). In the 3 highest age classes, the difference between bill and aggressive pecking in the proportion of forward-like forms is significant (resp. $\chi^2 = 10.2$, $p << 0.01$; $\chi^2 = 227,8$, $p < 0.01$; $\chi^2 = 76.4$, $p < 0.001$).

The orientation of aggressive pecks also changed with age. Fig. 4 gives the relative frequency of the places where young gulls hit the model or adult bird. In contrast to older gulls, which directed their pecks mostly to the bill or neck of the opponent (see also MANLEY, 1960), most of the pecks performed by gulls younger than 4 weeks of age hit the stimulus object elsewhere, for example on the wing or tail. The difference between the two age classes is significant ($\chi^2 = 38.62$, $p < 0.001$). It suggests that with increasing age the young became more precise in the orientation of

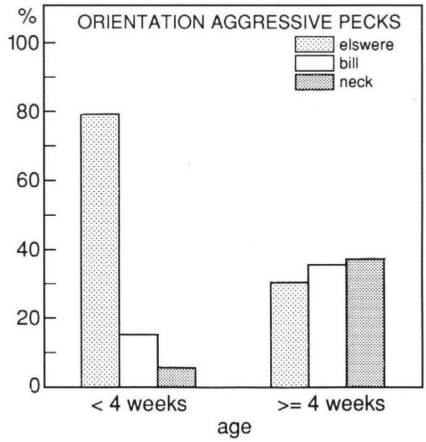

Fig. 4. The relative frequency of places where young birds of two age classes hit the stimulus objects during the standard stimulus experiments.

their aggressive pecks. This is in agreement with the impression that, in contrast to older gulls, young between the age of 2 and 4 weeks are very aggressive and run almost blindly towards the stimulus, without taking time to adjust their position relative to it.

b. *Fear behaviour: frequency of withdrawal and sitting.*

The average frequency of withdrawal and sitting as well as of aggressive pecks in the standard stimulus experiments of the large group are given in Fig. 5. Fear behaviour appeared before aggressive pecks were seen. Sitting decreased with age from the age of 5-7 days onwards, whereas withdrawal increased during the first 5 weeks. During the model experiments in weeks 5-7, the birds showed hardly any aggression, whereas withdrawal strongly increased. In contrast, both withdrawal and aggression decreased in frequency during this period in reaction to the living stimulus-bird. At the age at which the hand-raised young performed hardly any aggression anymore to the living intruder, young in the field leave their territories in the colony.

3a.2. Interaction between aggression and fear.

From the results presented above it is clear that aggressive and fear behaviour change with increasing age, both in frequency and form as well as in orientation. In this part the relation between aggression and

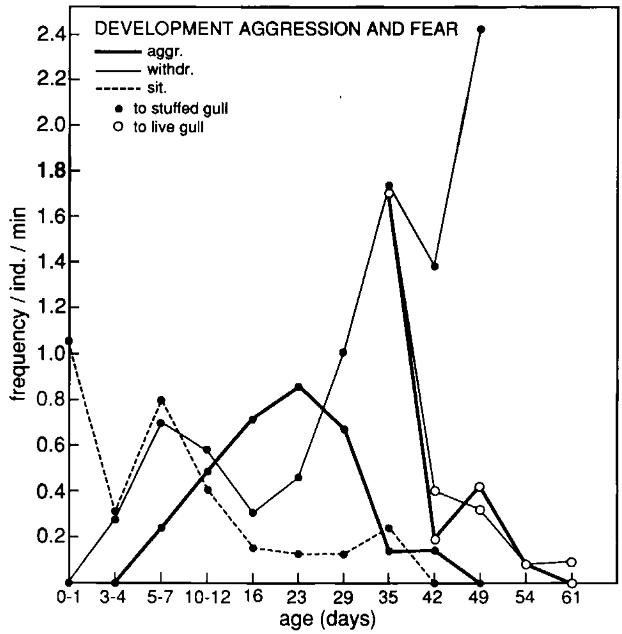

Fig. 5. Average frequency per bird per min of aggressive pecks (aggr), withdrawal (withdr) and sitting (sit), in standard stimulus experiments during ontogeny. Data are given both for experiments in which a stuffed black-headed gull and a live one was used.

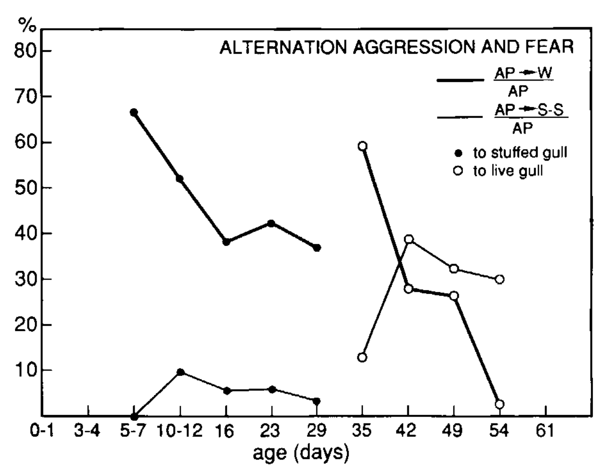

Fig. 6. Changes in the probabilities that aggressive approach (AP) is followed by withdrawal (W), or by stopping and standing-still (S-S) during ontogeny. Data are obtained from the standard stimulus experiments in large groups, in which either a stuffed adult gull, or a live one was used.

fear, as expressed in the temporal structure of locomotory behaviour will be considered.

Young, older than 1 week, almost always performed aggressive pecks when reaching the stimulus after approach. Therefore, approach can be interpreted as indicative of aggression. Withdrawal, at least in birds younger than 4 weeks, was very often followed by hiding, and can thus be considered as indicative of fear. Fig. 6 shows that in the experiments with a stuffed adult the percentage of approach combined with aggressive pecks that was immediately followed by withdrawal was high in young chicks but decreased with age. It increased in young of 5 weeks old, during their first confrontation with a living adult intruder, but then again decreased considerably in the course of ontogeny. As a consequence of the decrease in the proportion of aggressive approach immediately followed by withdrawal, the frequency of "stop" after approach increased. The thin line in the figure indicates that the relative frequency of approach, followed by stop and emerging in standing still, increased after the age of 5 weeks. As a result, the interactions of the young with the model lasted longer and lost their "unbalanced" appearance.

The increasing frequency of sudden stops after the aggressive approaches to the stimulus object suggests an increasing occurrence of an ambivalent agonistic motivation. It seems as if a tendency for aggression becomes inhibited by fear as the bird comes closer to the stimulus. This interpretaton is supported by the fact, that these stops after aggressive approach are more likely to be followed by withdrawal than was expected on the basis of random sequences ($p<0.02$).

The results of chi-square tests show that withdrawal was significantly more often followed by sitting than expected in case of random transitions ($p<0.001$). This sequence of moving away from the object, followed by crouching, very often while hiding in a shelter or between other young, strongly indicates that both are motivated by fear. On the other hand, sitting was more often than was expected followed by aggressive pecks ($p<0.001$). Thus sitting, like stopping, seemed to be squeezed in by overt aggression and overt fear behaviour. This indicates that during stopping, which increased in frequency during ontogeny, and during sitting both a tendency for aggression as well as a tendency for fear were activated in the bird.

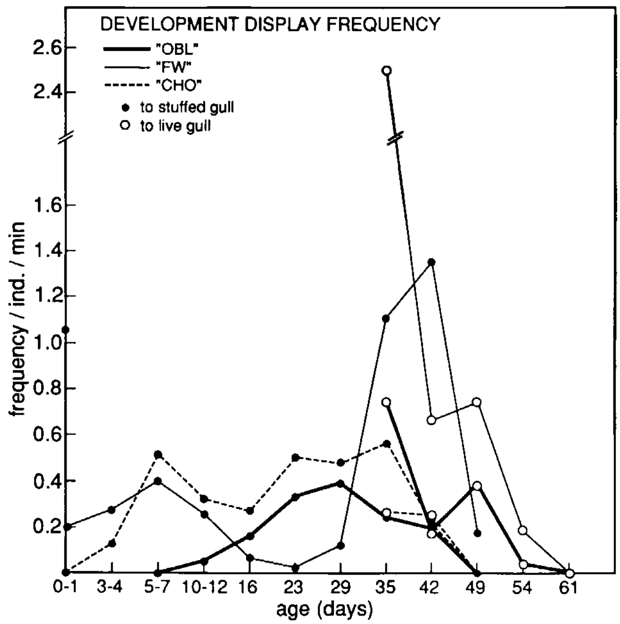

Fig. 7. Average frequency per individual per min of oblique-like ("OBL"), forward-like ("FW"), and choking-like ("CHO") postures in standard stimulus experiments during ontogeny. Results are given both for experiments in which a stuffed adult gull and a live one was used.

3a.3. Development of display behaviour.

Three types of displays were frequently seen during the standard stimulus experiments in the large groups: oblique-like, forward-like, and choking-like postures. The average frequencies in different age classes of these displays are depicted in Fig. 7. Forward-like, choking-like and oblique-like postures appeared in this order, and the frequency changes of each of them in the course of ontogeny showed a pattern, different from that of the other two.

These displays also gradually changed in form. Gulls, younger than 4 weeks of age, almost exclusively performed incomplete forms of these displays, whereas gulls, between 6 and 10 weeks old, performed complete postures in more than 60% of the cases. This form development has been extensively studied and quantified in an earlier study (GROOTHUIS, 1989; see Fig. 1).

3a.4. Relation between development of display and of overt aggressive and fear behaviour.

a. *Similarity in frequency changes during ontogeny.*

A comparison of the changes over time in frequency of display with those of overt aggressive and fear behaviour (compare Fig. 7 with Fig. 5), revealed that forward-like and choking-like postures appeared before aggression was seen, whereas oblique-like postures only were shown after aggression began to appear. This suggests that at least some development of aggression is necessary for the oblique-like postures to occur. Possible differences among the displays in their relationship with aggression, withdrawal and sitting were further investigated by comparing frequency changes during ontogeny of the former with those of the latter three. Similarities were quantified by means of Spearman-rank correlation-coefficients. These are given in Table 1. Indeed, the development in frequency of oblique-like postures correlated most strongly with the development of aggressive pecks. Choking-like postures correlated significantly with aggression, and almost significantly with the two forms of fear behaviour. Forward-like postures correlated only with fear. There was no significant correlation between the frequencies of aggression, withdrawal and sitting themselves. So, each of the three display types had its own relationship with overt aggressive- en fear behaviour.

TABLE 1. Spearman-rank correlation coefficients between the frequencies of overt aggressive and fear behaviour (see Fig. 5) and those of three displays (see Fig. 7) in the standard stimulus experiments during ontogeny

CORRELATION BETWEEN DEVELOPMENT OF DISPLAY AND OF AGONISTIC BEHAVIOUR

	'OBL'	'CH'	'FW'
A	0.78 **	0.58 *	0.12
W	0.36	0.50 (*)	0.51 *
S	-0.19	0.48 (*)	-0.06

(*) p<0.07
* p<0.05
** p<0.01

A = aggressive pecks; W = withdrawal; S = sitting; "OBL" = oblique-like postures; "CH" = choking-like postures; "FW" = forward-like postures.

b. *Timing of display during locomotion.*

Another way to investigate the motivational background of the three displays is to analyse the exact timing of these postures, relative to the locomotion pattern of the bird. The data obtained in 3a.2 indicate that during approach, which was often followed by overt aggression, during withdrawal, and during sitting and stopping, which both often occurred at the switch from aggressive approach and withdrawal, the bird is motivated by either aggression or fear or both. Standing still is the only category of locomotory behaviour for which an indication for activation of an agonistic motivation was not found. In Table 2 are given the frequencies of the displays and some other postures during approaching, stopping, standing still, withdrawal and sitting. Data of the different age-classes are taken together because between the classes no clear differences

TABLE 2. Observed (upper numbers) and expected frequencies of different postures during different categories of locomotion

DISPLAY AND LOCOMOTION

	APP	STO	STA	W	SIT	tot
'OBL'	38 28.0	137 46.3	52 89.7	35 78.1	6 25.9	268
'CH'	6 34.7	45 57.6	65 111.5	163 97.1	54 32.2	333
'FW'	76 63.6	100 105.4	206 204.2	223 177.8	5 59.0	610
AL	3 15.8	8 26.1	93 50.6	47 44.0	0 14.6	151
PUM	3 5.0	3 8.3	40 16.1	1 14.0	1 4.7	48
R	93 72.0	70 119.3	247 231.0	143 201.1	137 66.7	690
tot	219	363	703	612	203	2100

Observed data in double squares are significantly higher ($P<0.05$) than was expected on the basis of a random distribution. Data are obtained from standard stimulus experiments (model as well as a live stimulus), in large groups of young gulls between the age of 1 and 10 weeks. "OBL" = oblique-like postures; "CHO" = choking-like postures; "FW" = forward-like postures; AL = alert; PUM = pumping; R = all other postures (mainly normal rest posture); TOT = total; APP = approach; STO = stop; STA = stand still; W = withdrawal; SIT = sit.

with respect to timing during locomotion were found. The distributions of the postures observed differed significantly from random.

Let us first consider those postures which were relatively frequently performed during the "neutral" standing still. These are the pumping display and the alert posture. This suggests that these two motor patterns cannot be classified as clearly agonistic postures. This conclusion is supported by the following observations. In the field, pumping was almost exclusively performed during begging by young towards their parents. I never observed aggressive pecking immediately after the pumping display. Moreover, there was no correlation between ontogenetic changes in frequency of pumping and those of aggressive pecking (data obtained from mutual interactions). The alert was performed in all kinds of contexts, during all sorts of disturbances in the surroundings of the bird as well as during begging.

In contrast, the oblique, forward and choking displays were relatively frequently performed during other categories than the "neutral" standing still. They were relatively often performed during stopping, withdrawal and sitting. But there are also differences among these displays in their distribution in this matrix. The oblique-like display was performed significantly more often than expected during stopping, whereas choking-like postures occurred more often during withdrawal and sitting, and forward-like postures during withdrawal. In 3.2 it was suggested that stopping and sitting were controlled by both an internal variable for aggression and one for fear. If this is true it seems likely that also the oblique-like postures, performed during stop, and the choking-like postures, performed during sitting, are motivated by these two internal factors. No evidence was obtained that the forward-like postures are under the direct influence of aggression: they rather seem to be controlled by an internal factor for escape.

The relatively high frequency of the remaining postures (R) during approach is partly due to the fact that erect postures lasting too shortly to be classified as oblique-like display, fell in this "R"-category. These "postures" were often a preparation for attack, but could become real oblique-like postures, performed with long-call-like vocalizations when the bird stopped in front of the model. This is in line with the idea that oblique display is (partly) motivated by aggression inhibited by fear. The relatively high frequency of the R-postures during sitting can partly be attributed to the fact that during sitting often incomplete forms of choking display occurred. Part of these postures could only be distinguished from R-postures by the occurrence of choking-like vocalizations, and not by the form of the posture itself. They were therefore classified as R-postures, occurring during sitting.

c. *Form development of display and probability of attack.*

One of the main arguments in favour of the conflict hypothesis is the finding that in the form of some displays, elements of both overt aggressive and overt fear behaviour seem to be present. In the black-headed gull the form of the erect, oblique-like postures has the greatest similarity to overt aggression: the erect aggressive pecks. Therefore it was expected that oblique-like postures would have more often sequential links with overt aggression than forward-like or choking-like postures. To test this, the strength of the connection between attack and several sub-forms of the three displays: oblique, forward and choking was calculated. These are depicted in Fig. 8. Considering the means of the scores of all subforms for each display (in Fig. 8 marked with an arrow), the oblique-like postures indeed were found to occur more often than the other displays just before or after attack ($\chi^2 = 105.9$, df = 3, $p<0.001$).

During ontogeny, the form of the displays changed from what is called incomplete or transitional forms of display, typical for young gulls, to

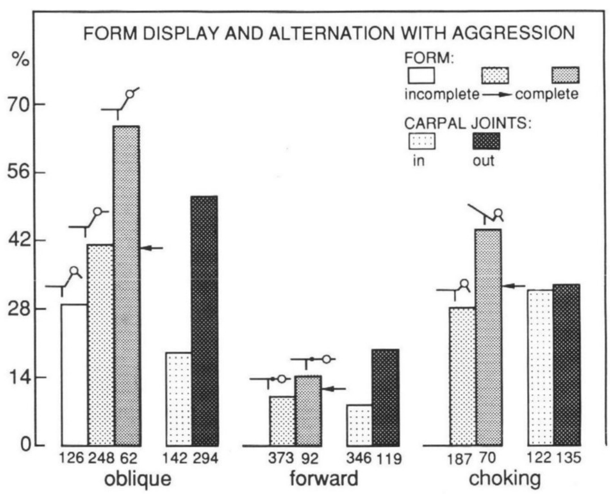

Fig. 8. Percentage of (sub)-forms of display, immediately followed by, or immediately following aggressive pecking of the same subject. The data concern different bill positions in the oblique (bill pointing downwards, horizontally and upwards), different positions of the neck in the forward (not extended and extended), different positions of the body in choking (horizontal and tilted to the ground) and different positions of the carpal joints (close to, and extended from the body). Arrows mark the mean scores over all sub-forms of one display.

complete adult forms. The oblique-like postures were more and more often performed with a bill, pointing horizontally or upwards; the forward was more frequently performed with a partially extended neck; the relative frequency of choking-like postures in which the body is tilted increased and finally, all three displays were more often performed with extended carpal joints (see also GROOTHUIS, 1989). In most cases, the complete form had more often sequential links with overt aggression than the incomplete display (for the effect of bill position in the oblique: $\chi^2 = 22.27$, df = 2, $p < 0.001$; for the carpal joints position in the oblique: $\chi^2 = 39.36$, df = 1, p = < 0.001; neck position in the forward: $\chi^2 = .81$, df = 1, n.s.; carpal joints position in the forward: $\chi^2 = 12.6$, df = 1, $p < 0.001$; body position in choking: $\chi^2 = 5.18$, df = 1, $p < 0.02$; carpal joints position in choking: $\chi^2 = 0.1$, df = 1, n.s.).

Not only the development of sequences between display and aggression but also that of the oblique-forward is of interest. The alternation of these two displays is the most stereotyped sequence in the display behaviour in adult black-headed gulls. In Fig. 9a is plotted the percentage of oblique-like postures immediately followed by forward-like postures, for four age classes of young gulls. This percentage was very low in gulls younger than 5 weeks of age (significantly lower than was expected on the basis of random transitions between the postures), but

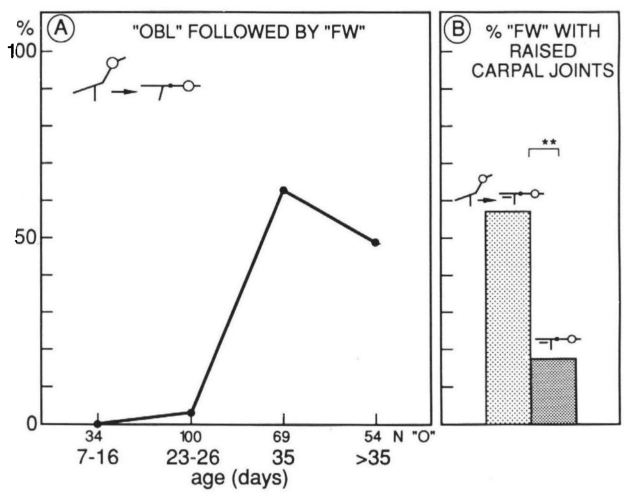

Fig. 9. A. The percentage of oblique-like postures immediately followed by forward-like postures, for 4 age classes of young gulls. B. The percentage of forward-like postures, performed with raised carpal joints, when this posture followed the oblique and when it was performed in other sequences.

it increased considerably thereafter. In the two highest age classes this sequence occurred significantly more often than expected.

The finding that forward-like postures, often performed during withdrawal, became linked in sequence with the more aggressive oblique, may appear puzzling. However, as can be deduced from Fig. 9b, forward-like postures following the oblique, more often exhibited raised carpal joints than forward-like postures in other sequences. So, especially the aggressive form of the forward became relatively often coupled with the aggressive oblique.

3a.5. The effect of manipulation of aggression on the performance of display behaviour.

The effect of testosterone on the frequency of aggressive behaviour and display behaviour is presented in Table 3. Fear behaviour, more difficult to score than aggressive pecks, was not quantified. Birds, treated with testosterone, performed aggressive pecks on the standard stimulus more frequently than control birds. More importantly, the more aggression a bird performed, the more display it showed. These displays consisted of oblique-like, forward-like and choking-like postures. Begging display was hardly seen anymore in young treated with testosterone.

TABLE 3. Relation between frequency of display (D) and frequency of aggressive pecks (A) of the same bird during the same experiment

chicks with **<u>testos-impl</u>** and controls

D \ A	0	1-3	>3
0	25	1	1
1-3		1 <u>3</u>	
>3			<u>9</u>

Frequency of behaviour is scored in 3 classes: 0, 1-3, and more than 3 per experiment. Results obtained from experiments in which a stuffed black-headed gull was introduced in the home cage of small groups of 5-14 days old chicks, of which some individuals were implanted with a pellet testosterone proprionate. The scores of the latter are underlined.

This finding indicates that the three displays: oblique, forward and choking, for which evidence was obtained that they develop in relation with motivational factors for agonistic behaviour, indeed share a common causal factor with overt aggressive behaviour.

3b. Agonistic behaviour in older birds: mutual interactions.

3b.1. Changes in frequency of aggression, fear and display. Birds were considered to be involved in an agonistic interaction if at least one of the participants showed at least overt aggression or oblique, forward or choking display. The average frequency per interaction per bird of withdrawal, overt aggression and display during agonistic interactions with birds of the same age is presented in Fig. 10 for 3 age classes of gulls. It shows that in older birds, withdrawal and overt aggression decreased, while display increased in frequency. Part of the withdrawal movements consisted of walking or running away from the other bird, often in reaction to aggression of the opponent. The proportion of extreme

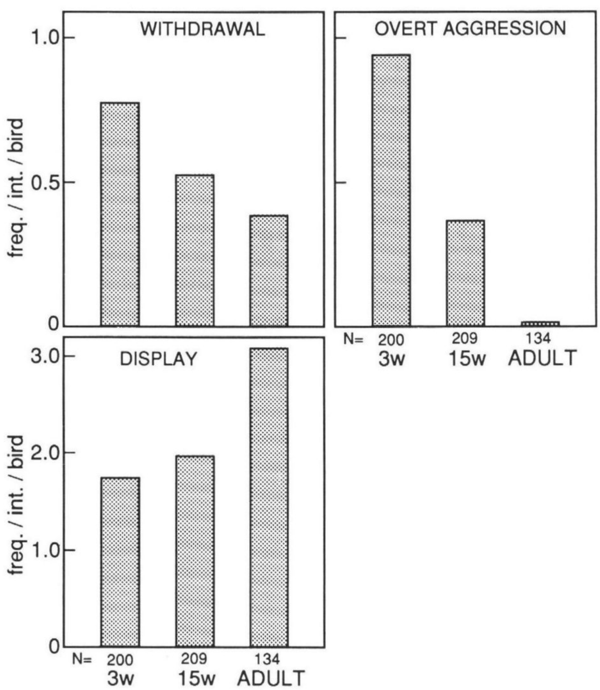

Fig. 10. Frequency per agonistic interaction per bird of withdrawal, overt aggression and display for 3 age classes of black-headed gulls. N = total number of interactions analyzed.

withdrawal in all withdrawal movements also decreased with age, from 79% (n = 156) via 47% (n = 108) to 39% (n = 51): $\chi^2 = 41.46$, $p < 0.0001$).

Thus, during ontogeny, the frequency of overt expression of fear and aggression decreased while the frequency of display went up. As a consequence, the proportion of display behaviour in relation to aggressive behaviour showed a significant rise ($p < 0.01$).

The oblique display is the most frequently performed display in adult black-headed gulls. In part 3a4c it was concluded that this posture had by far the strongest connection with aggression in comparison with the other displays. To analyse a possible shift in agonistic behaviour from overt aggression to agonistic display, the frequency of oblique-like postures during agonistic interactions (O), was related to that of aggressive pecks (A). The ratio O/(O + A) is given in Fig. 11 for two types of interactions:

1. of birds with conspecifics of the same age;
2. of young gulls with the standard stimulus.

Both curves clearly rise with age, suggesting that overt aggression became more and more replaced by display. Three weeks old birds, in interaction with conspecifics, showed a higher proportion of display than in the standard stimulus experiments. This might be explained by the fact that the birds were more intimidated by a live conspecific, exhibiting

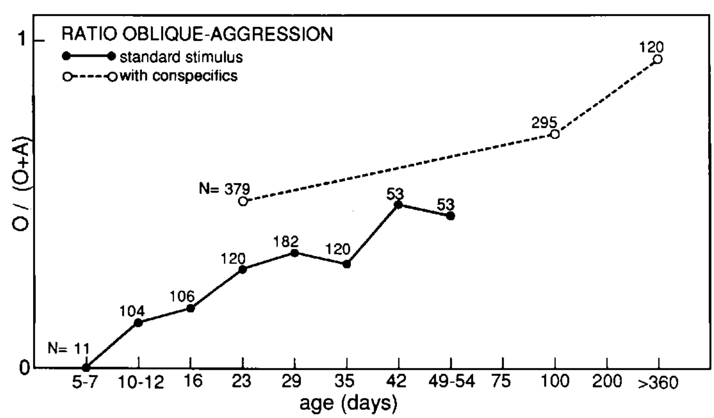

Fig. 11. Frequency of oblique-like postures (O), divided by this frequency plus the frequency of aggressive pecks (A), for young of different ages in two different contexts: standard stimulus experiments and interactions with conspecifics of the same age.

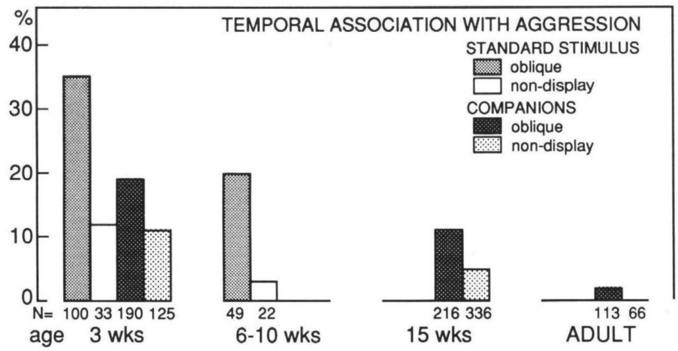

Fig. 12. Percentage of postures, classified as either oblique-like display or non-display, immediately followed by aggressive pecks, for young of different age classes. Scores are obtained in two different contexts: standard stimulus experiments and interactions with conspecifics of the same age (companions).

display and aggressive behaviour, than by the neutral standard stimulus object.

As a consequence of the shift from aggressive behaviour to display behaviour, the percentage of oblique display that was immediately followed by attack or an intention movement to attack, decreased in both types of interactions during ontogeny. In Fig. 12 it can be seen that, despite this decrease, the oblique postures still maintained a stronger connection with overt aggression than other postures, not classified as being displays. Differences between these two categories of postures, were tested with the chi-square tests. Significant differences were found ($p < 0.05$) in data of both age classes of the standard stimulus experiments and in data obtained from mutual interactions of 15 weeks old gulls. The continued association between aggression and display is also apparent in the fact that I hardly observed aggressive pecks not preceded or followed by display, even in adults.

3b.2. Changes in timing and context of display.

The decrease in overt aggressive behaviour during ontogeny makes it difficult to establish the possible existence of a common causal factor for aggression and display behaviour in older birds. It is conceivable that in these birds, despite the decrease in frequency of overt aggression, the motivation for aggression is still activated but that its expression is suppressed through inhibition by other active internal factors. One way of studying the relationship of aggression with display, more or less independently from the previous one, has been presented in section 3a.4: the analysis of the occurrence of the different postures during the different locomotion categories. These data on young gulls were obtained from stadard stimulus experiments. In contrast, data on adult behaviour were obtained from mutual interactions. To make both data sets comparable, only those interactions between adults were used in which one of the opponents behaved more or less neutral, showing no overt aggression or fear behaviour.

The results are presented in Table 4. In contrast to young gulls (Table 2), adult gulls performed the oblique and forward display not during stopping or withdrawal, but frequently during approach. Choking was hardly seen anymore, and sitting did not occur at all. The alert and pumping movements are lumped together in the rest category. Moreover, approach in adults mainly consisted of quietly walking towards the other bird, not followed by attack, while approach in young birds often consisted of running towards the stimulus object, followed by overt aggression. Comparison of the results obtained from young gulls and from adults strongly suggests, that the motivation underlying the displays changes during ontogeny.

TABLE 4. Observed (upper numbers) and expected frequencies of different postures during different categories of locomotion

DISPLAY AND LOCOMOTION: ADULTS

	APP	STO	STA	W	tot
OBL	$\boxed{61}$ 43,0	25 25.2	18 28.6	9 16.1	113
CHO	1 8.8	7 5.1	8 5.8	7 3.3	23
FW	$\boxed{85}$ 54.8	16 32.2	34 36.5	9 20.5	144
R	32 72.3	57 42.5	59 48.1	42 27.0	190
tot	179	105	119	67	470

Observed data in double squares are significantly higher ($p<0.05$) than expected on the basis of a random distribution. For abbreviations see Table 2.

Another important feature of timing of displays in black-headed gulls concerns the adjustment in the performance of oblique and forward postures to the displays exhibited by the opponent. In 3a.5 it was shown that the percentage of oblique postures that was immediately followed by the forward, increased with age. Adult gulls not only often alternate these two postures, they also performed the oblique-forward sequences synchronously with those of the opponent (MANLEY, 1960; VAN RHIJN, 1981). To find out whether the amount of synchronisation changed in the course of ontogeny the percentage of oblique- or forward-like postures that was performed synchronously with the same posture of the opponent was calculated for 3 age classes of gulls. Whether the birds synchronously performed display more often than was expected on the basis of performance, independent from the display of the opponent, was tested with a chi-square test. The results are presented in Table 5. The relative frequency of synchronously performed display considerably increased during ontogeny, as did the value of χ^2 ($p<0.05$ for all 3 age classes). So, older birds time their display more precisely with those of the opponent.

Although the distribution of the displays over different social contexts was not quantified, it was very obvious that display performance in adult gulls, in contrast to young, was not restricted to clearly agonistic situations. Gulls younger than 6 months performed complete forms of the oblique, forward and choking only to intruders on their territory and never to their siblings or parents. In contrast, adult gulls frequently used these displays during pair formation, to their partner at the time the pair bond is well established, and to call their young. In the last two situations, aggression was never seen. Adult black-headed gulls frequently

TABLE 5. Percentage of oblique and forward postures simultaneously performed with the same display of the opponent, for three age classes of gulls

	6 WEEK	12 WEEK	ADULT
OBL	15 (52)	33 (48)	42 (76)
FW	16 (56)	60 (20)	54 (52)
X^2	12.05	28.77	62.83

Sample seize in brackets.

performed the oblique and forward displays during nest reliefs also. Regularly the partner on the nest refused to leave in response to display on the newly arrived partner. The latter may then try to push its partner from the nest or to sit on its back; but even in these cases I never saw overt aggression.

The increase of synchronous performance of display and the widening of the context of these displays in the course of ontogeny suggest that the execution of these displays gradually becomes more dependent on specific external stimulation and probably more independent of a specific internal state.

4. Discussion

4.1. Development of internal factors for aggression and fear.

Two forms of fear behaviour could be distinguished: withdrawal and sitting, the latter often while hiding. Two such types of behaviour were also found in Junglefowl chicks by HOGAN (1965), which he named withdrawal and freezing. He postulated two behavioural systems for the control of these patterns: withdrawal and fear respectively. CARLSTEAD (1983) also found two forms of fear behaviour in cichlid fish, which she named avoiding and hiding. She extensively discussed the organization of fear behaviour in animals. In contrast to HOGAN, CARLSTEAD interpreted the occurrence of two forms of fear behaviour as the result of different types of external influences on one internal mechanism. However, in her model explaining the causal organization of agonistic behaviour in cichlid fish she felt it necessary to postulate beside this mechanism a separate system for responding to disturbances, influencing the type of fear behaviour shown by the fish. Thus in her conception also two different internal mechanisms are involved in the control of two different motor patterns which can both be classified on functional grounds as fear behaviour. The finding that in young gulls the frequency of withdrawal and of hiding change in different ways during ontogeny (Fig. 5), strongly speaks for this idea. In the discussion below, these two internal factors, together controlling fear behaviour in young gulls, will be called escape and hiding.

Several authors have postulated a tendency "to stay put" as an separate internal factor involved in the control of display behaviour in birds (BAERENDS & VAN DE CINGEL, 1962; BLURTON JONES, 1968) or colour patterns in cichlid fish (BALDACINI, 1973). A tendency to stay on the same place is a characteristic of hiding behaviour also. Therefore, it may be that this type of fear behaviour is motivated by a tendency to stay put, which in turn is activated by fear. During hiding, young chicks often perform choking-like postures, indicating that these displays are motivated also by both tendencies for fear and to stay put. However, older young performed these postures more and more outside a shelter, on the territory in front of the intruder. Moreover, adult gulls perform the display mainly on the nest site, indicating that choking is performed when the bird is strongly attached to a particular place. These findings suggest that in the course of ontogeny fear gradually influences the occurrence of choking less strongly, while the tendency to stay put becomes more prominent. Such a shift in context from hiding to staying put openly in front of the opponent is also noticed by HULSCHER-EMEIS (pers. comm.) for the occurrence of vertical bars in the colour pattern of a cichlid fish.

In the gulls, fear and aggressive behaviour developed in this order (Fig. 5). KRUIJT (1964) also found this in young fowl. The hypothesis that the two types of behaviour are controlled by at least two different internal factors is supported by the fact that the course of their changes in frequency during ontogeny are not similar (Fig. 5). These factors must be considered to be internal ones, because of the following two findings. Despite the fact that the external stimulus remained more or less constant (standard stimulus experiments), aggressive pecking, withdrawal and sitting changed in frequency and form (Figs 5 and 3) during ontogeny, as well as in the course of one experiment. Furthermore, these behaviours persisted even after the stimulus had been removed.

As the birds grow older, the internal factors for aggression and fear seem to become simultaneously aroused more often. KRUIJT (1964) has suggested this also for the ontogeny of social behaviour in Burmese red junglefowl. In the gulls, simultaneous arousal is indicated by the following three findings:

1. In the form of the displays, elements considered as representative for aggression were more often simultaneously present with those, indicative for fear: this will be extensively discussed below.

2. Aggressive approach and aggressive pecks became less often followed by withdrawal (Fig. 6). As a consequence, the agonistic behaviour of the young birds lost its unstable, vacillating appearance. The interactions persisted longer and the frequency of stopping, after aggressive approach, increased. Because stopping and sitting were squeezed in between two opposite motor patterns, aggressive approach and withdrawal, (section 3.2), it might be that both stopping and sitting are expressions of simultaneous activation of internal factors for aggression

and fear. This simultaneous activation of two opposite tendencies thus leads to a kind of stalemate situation, in which neither overt aggression nor overt fear behaviour can come to expression.

3. The percentage of incomplete aggressive pecks increased during ontogeny (Fig. 2). Thus in older birds overt aggressive behaviour seemed to become inhibited by an opposite tendency, most likely fear (Fig. 2). Such a shift during ontogeny from uninhibited overt aggression to less pronounced aggression has been found by several authors: *e.g.* BAERENDS-VAN ROON & BAERENDS (1979) for the behaviour of cats; KRUIJT (1964) for the behaviour of cocks; MCLEOD (cited in FENTRESS & MCLEOD, 1987) for the behaviour of wolves; OHM (1964) for the behaviour of cichlid fish.

The increasing inhibition of aggression by fear may seem contradictory to the concluson presented above that in the course of ontogeny fear developed before aggression. However one must realize that the development of internal factors for behaviour and the development of the interaction between these factors are two different phenomena. One of the interesting findings is that in the ontogeny of behaviour first separate internal factors for different behaviour patterns develop, which seem to control behaviour more or less independently from each other, before they influence their mutual expression in the final behavioural output.

It must be noted that the total frequency of aggressive pecks decreased during the period that the percentage incomplete pecks, or intention movements to peck, increased (Fig. 2). This makes it necessary to consider whether the increase of intention pecks might be explained by a decrease in the activation of an internal factor for aggression alone instead of by this factor, inhibited in its expression by fear. However, if this were the case, one should also expect: 1. a high percentage of intention pecks early in ontogeny, at the time the motivation for aggression is not yet very strongly developed, and 2. a gradual decrease in relative frequency of these pecks during the period that the motivation for aggressive behaviour increases (the first 4 weeks of age). These expectations were not fulfilled. Consequently two variables have to be assumed to explain the change in percentage of intention aggressive pecks.

A final remark should be made on the relation between the causation of bill pecking and aggressive pecking. In older young, bill pecking is clearly related to begging behaviour and motivated by hunger (*e.g.* HAILMAN, 1968), whereas there is no evidence that in birds of this age aggressive pecks are motivated by hunger. However, the influence of an internal factor on bill pecking in very young chicks is less clear. Bill pecking in a few days old gull chick seems to be independent from such a hunger factor (Hailman, 1968), like early ground pecking in junglefowl chicks (Hogan, 1987). The form and force of very early bill pecking is quite similar to that of early aggressive pecking, although the former is more preferentially directed to bill shaped objects. Whether early bill and aggressive pecks have a factor controlling aggressive behaviour in common remains a point for further study.

4.2. Display development.

Three of the four main displays in young black-headed gulls, the oblique, the forward and choking, share at least one common causal factor with either overt aggressive or overt fear behaviour or both. This conclusion is based on the following results:

1. The three displays were almost exclusively performed in a clearly agonistic context, in which plenty of overt aggressive and fear behaviour was performed.
2. The displays changed in frequency during ontogeny, in correspondence with changes in frequency of aggressive and/or fear behaviour (Table 1).
3. The displays were often linked in sequence with overt aggressive behaviour, or performed during overt fear behaviour (Fig. 8 resp. Table 2).
4. Testosterone is an important internal common causal factor for aggressive and display behaviour, because it stimulated the frequency of both types of behaviour (Table 3).

Whether testosterone acts directly on the performance of display behaviour, or via another intervening variable for agonistic behaviour, is not yet clear. The finding that in the displays some form elements, characteristic for overt aggression were present, suggests that testosterone stimulates the activation of a more specific internal factor, controlling aggressive behaviour, which in turn influences display behaviour. This point needs further study.

Thus, internal factors controlling aggressive and fear behaviour are involved in display development. Moreover, these factors seem to be activated simultaneously during the performance of the displays. For the oblique and choking displays this follows from the finding that these postures were relatively often performed during stopping, respectively sitting (Table 2). Both stopping and sitting were likely to be controlled by both "aggression" and "fear" (see above). For the forward, this can be deduced from the findings that this posture occurred frequently during withdrawal, while it also alternated with the aggressive oblique display (Fig. 9).

In the course of ontogeny both types of fear behaviour, withdrawal and crouching, appeared before aggressive pecks were seen (Fig. 5). This may indicate that the display patterns develop from fear behaviour, by addition of behavioural elements, typical for aggression. This idea is strongly supported by the development of the form of these displays (GROOTHUIS, 1989; Fig. 1).

In the following I shall substantiate this statement for each of the displays separately.

The complete adult *choking* posture has its developmental origin in the crouching posture, performed by chicks while hiding in the vegetation. During ontogeny, this posture is more and more often performed together with vocalizations, typical for choking. The form of this crouching fear posture changes gradually, by an addition of at least four form elements, characteristic for activated aggression (while the posture is still often performed during withdrawal and sitting), viz.:

1. In the course of ontogeny the bill was more often held downwards, often while the bird made rapid pecks to the ground with a small amplitude. Because aggression regularly followed choking immediately (Fig. 8), and no other pecking movements were seen in this context, this form element was interpreted as redirected aggressive pecking.

2. The carpal joints were more often held away from the body, as was almost always the case during aggressive pecking in young gulls.

3. The body was more frequently tilted towards the ground, as the consequence of stretching the legs; it seems as if the bird is preparing itself for leaping towards the opponent. This interpretation is supported by the relatively high probability of subsequent attack when the bird performed choking with the body tilted (Fig. 8).

4. Older young performed the posture frequently in front of the threatening stimulus, instead of during hiding in the vegetation.

In this ontogenetic study no evidence was obtained to support a suggestion made by TINBERGEN (1959) that head-movements in choking originate from displacement nest building or displacement regurgitating. Neither nest building movements nor regurgitating were seen in young gulls at the age they already performed complete choking.

During ontogeny, the form of *oblique*-like postures gradually develops from crouching or choking-like postures to erect displays. This has been extensively discussed by GROOTHUIS (1989). This change in form is likely to be due to an increasing influence of a tendency to behave aggressively, and a decreasing influence of a tendency to stay put. This follows from the following findings:

1. The form of overt aggression consists of erect movements (Fig. 3) often accompanied by extended carpal joints. When the threatening stimulus came close, the crouching or choking bird prepared itself for overt aggression, moving its head upwards and extending the carpal joints.

2. This change in posture was often followed by running towards the stimulus object in an erect posture. Then the birds suddenly stopped and more or less freezed in this posture (Table 2) resulting in the performance of oblique-like poses, which gradually increased in duration (GROOTHUIS, 1989).

3. The course of changes in frequency of erect oblique-like postures during ontogeny correlated more strongly with those of aggression than the course of changes of choking-like postures did (Table 1). Furthermore, oblique-like postures were more often linked in sequence with attack than choking-like postures (Fig. 8). Moreover, oblique-like postures were more often performed in sequence with aggressive pecks when the bill pointed upwards instead of downwards, the latter being the case in choking and in early forms of oblique-like postures (Fig. 8).

The *forward* develops from a posture in which the neck is withdrawn between the shoulders, to a posture in which the neck is extended forwards and the carpal joints are raised. The incomplete form of the forward is clearly motivated by a tendency to escape: young gulls often tried to escape in this hunched posture, and the frequency changes of this motor pattern during ontogeny correlated strongly with those of withdrawal (Table 1). The addition of raised carpal joints suggests the simultaneous presence of an aggressive motivation in the posture. This is also indicated by the fact that the complete forward was more often linked in sequence with attack and with the oblique than the incomplete one (Figs 8 and 9b).

In conclusion, the changes in form and frequency of the three agonistic displays during ontogeny can be seen as the consequence of a development in motivational factors for aggression, escape and hiding, which increasingly interact with each other as the birds grow older. However, it must be realised that the different motivational states of the animal can only trigger a limited number of already existing species-specific possibilities for motor output. If this were not so, much more variation in the form of the postures should have occurred during the course of ontogeny (see Fig. 13a, b).

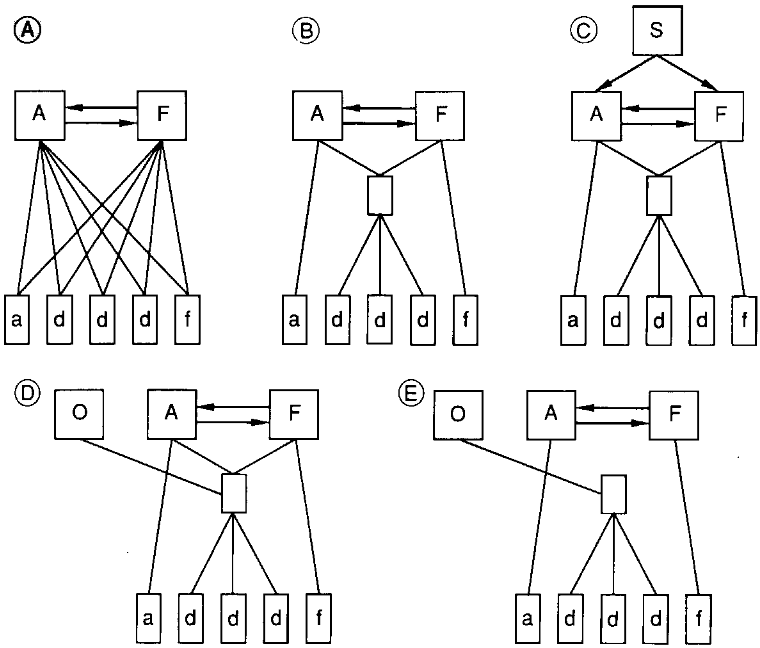

Fig. 13. Models, depicting possible explanations of the causal organisation of display behaviour. The large squares represent internal factors, the small rectangles motor patterns. A = aggression; S = sex; F = fear; O = other motivational factor; a = overt aggression; d = display; f = overt fear behaviour (after BAERENDS, 1955 and KRUIJT, 1964). A: displays are controlled directly by A and F. B: A and F control display behaviour via a third intervening variable. The latter triggers the different displays, according to its input from A and F, and can account for the stereotypy of displays, regardless of some fluctuations in motivational state. C: A third system for sexual behaviour stabilizes the interaction between A and F. See text. D: Extension of motivational factors controlling display behaviour; see text. E: Emancipation of display behaviour; see text.

A remark must be made on the motivational background of the *pumping* display. There is no evidence that this display is under the control of aggression. The frequency of this display was not limited to agonistic situations. In the standard stimulus experiments the display was relatively frequently performed during the "neutral" standing still, in contrast to the agonistic displays (Table 1). Moreover, pumping decreased in frequency in birds implanted with testosterone. The form of the posture consists of a rapid alternation of the alert posture with incomplete forms of the forward (Fig. 1). Both pumping and the alert posture increased in frequency when birds, for some time deprived of food, saw or heard the animal care-taker. This suggests that an internal variable, "hunger" stimulates the alertness of the bird, which then in turn affects pumping.

The other form component of pumping, the incomplete forward, is especially pronounced in what has been called "low-pumping", the pumping-type characteristic for older young (GROOTHUIS, 1989). This suggests that during this low-pumping the dominating motivation of the incomplete forward, escape (see above), is present. Indeed, I had the impression that young, performing pumping with a pronounced horizontal component in the display, were relatively "cautious" in approaching the animal care-taker. In the field, this low-pumping was often performed by older young while approaching their parents. In this context the presence of the forward-like escape component in pumping may be explained by two factors:

1. Older young very often had to cross neighbouring territories during the approach, which may stimulate the escape tendency in the bird;
2. Young get increasing experience with attacks from adult gulls and may associate their adult parents increasingly with a threatening stimulus.

It is not my intention to suggest that every pumping movement is caused by successive ambivalence of "alertness" and escape. The stereotypy of this display must imply a pattern coordinator for motor output of its own, although sensitive for motivational changes (see also Fig. 13a, b).

4.3. Motivation of adult display.

In the foregoing section it was concluded that the species-specific displays of black-headed gulls change in form and frequency during ontogeny under the influence of changes in the motivational factors for aggressive and fear behaviour. The data underlying this conclusion were obtained from gulls, younger than the age of 10 weeks. However, the results presented in section 3b indicate that the organization of display behaviour changed in birds, older than 10 weeks, after the development of the displays had been completed. I shall elaborate on this in the following discussion.

In comparison to young gulls, adults show little overt aggressive and fear behaviour and frequently perform displays (Fig. 10). Even the most aggressive display in young birds, the oblique, is rarely followed by aggression in adults (Fig. 12). Consequently the question needs to be considered whether in adult gulls displays are still motivated by internal factors for aggression and fear. One might answer this question positively if one assumes that the changes in agonistic behaviour during late ontogeny are the result of the increasing interaction between internal factors for aggressive and fear behaviour, also postulated for the display development in young gulls (section 5.1). Mutual inhibition by these factors on each other's expression in the final motor output might cause a decrease in frequency of overt expression of aggression and fear, and an increase in ambivalently motivated display. This explanation was suggested by KRUIJT (1964) for the development of agonistic behaviour in Burmese red junglefowl. In this way the change in agonistic behaviour in gulls, older than 10 weeks would be the result of a change in the behavioural organization, already started in the beginning of ontogeny, since already in young gulls agonistic behaviour gradually shifted in properties to characteristics of adult behaviour (Figs 11 and 12).

However, in adult display behaviour important properties were found, not present in display behaviour of young gulls. One of these is its occurrence outside an agonistic context (section 3b.2). The appearance of agonistic displays in sexual encounters, as well as a considerable decrease in frequency of overt aggression in the course of ontogeny was also found by KRUIJT (1964) in Burmese red junglefowl. He suggested that the increase in interaction between two behavioural "systems", controlling aggression and fear behaviour, becomes stabilized during ontogeny partly as the consequence of the development of a system for sexual behaviour (Fig. 13c). Due to the effect of this third system on the systems for aggression and fear, overt aggression and fear behaviour are seldom activated anymore. Display behaviour, on the other hand, increases in frequency as the consequence of interaction between both systems, and appear in sexual encounters. Indeed, in junglefowl, sexual behaviour developed gradually at the time overt attack behaviour decreased. However, this is not the case in the black-headed gull: neither the upright display with head-flagging, typical for sexual encounters in this species, nor copulations were seen in young birds. Even one-year old gulls rarely performed these behaviour patterns. Moreover, chicks that were implanted with testosterone sometimes showed copulatory behaviour, but this was never accompanied with the displays they performed in an agonistic context. Therefore, the development of a system for sexual behaviour cannot account for the shift in social behaviour from overt aggression to display behaviour in the course of ontogeny.

In fact, adult black-headed gulls performed so little overt aggressive behaviour during social interactions, and performed displays so frequently outside a clearly agonistic situation, that one has to consider the alternative explanation that adult display is not always controlled by internal factors for fear and aggression. This idea is in contradiction with the one advocated by BAERENDS (1975). He considered it likely that in almost every social encounter between conspecifics tendencies for agonistic behaviour will be activated. His idea was based on the fact that the same displays occurring in clearly agonistic interactions are also performed in other contexts, such as sexual encounters. He felt it more parsimonious to assume that in these different contexts the same displays are controlled by the same motivational systems, than to postulate for different contexts different motivational states for the occurrence of the same display. BAERENDS' idea is in line with suggestions of MOYNIHAN (1955). This author has reported aggression of males to females, especially in the beginning of the season. This seems to indicate that in sexual encounters the tendencies for agonistic behaviour are activated: unknown females arouse aggression in courting males, and the activation of aggression in males decreases by the time the partners become familiar with each other and display frequency also drops (see also MANLEY, 1960). However, in our colony of adult black-headed gulls at the laboratory, in which all birds were individually recognizable, we only saw aggression of males towards approaching females in cases the male did not accept the female as a partner (mainly occurring in the beginning of the season). Males did not react aggressively to unknown females which they did not reject, and to these they frequently addressed displays (GROOTHUIS & VAN RHIJN, pers. obs.). Furthermore, in encounters between mates of a well established pair, or between parents and their young, I have never observed signs of tendencies to attack or to flee. In my opinion the hypothesis of BAERENDS has to be rejected in view of these new findings. I consider the widening of the context for display behaviour in older birds as an indication that display in adults is not always motivated by tendencies for agonistic behaviour. The occurrence of the same display in different contexts, in which the probability of subsequent attack varies greatly, is also reported by VEEN (1987) for adult little gulls.

Except for the decrease in frequency of aggressive and fear behaviour, and the widening of the context of display, two types of data support my interpretation that the motivational background of the latter change during ontogeny:

1. Young birds often performed displays during stopping and sitting (Table 2). This fact, used as evidence for the hypothesis that displays are

controlled by a simultaneous activation of aggression and fear did not hold for the behaviour of adult gulls. They performed display relatively often during (quiet) approach (Table 4).
2. The increase in synchronously performed display (Table 3) seems only possible when the performance of these motor patterns become gradually more independent of an internal state involving a specific attack/escape balance. It seems not very likely that two opponents, performing the typical oblique-forward sequence synchronously, have almost exactly the same motivational state, changing simultaneously during an interaction.

In conclusion, internal factors controlling overt aggressive and fear behaviour influence display development in black-headed gulls, but are not always involved anymore in the control of display in adult gulls. It seems as if these displays, once developed and fixed in form, become subroutines, that can be employed in several behavioural programmes. The term "emancipation" was originally coined for the evolutionary process in which the original control of a particular motor pattern by a particular motivational factor was taken over by another one (TINBERGEN, 1952) (Fig. 13e). The same kind of changes seem to take place in the ontogeny of the species-specific displays of the black-headed gull. However, if aggression is shown by adult gulls, in most cases display is shown also. Therefore it must be concluded that the original connection between the display and internal factors controlling overt aggressive and fear behaviour still exists in adult gulls, despite the fact that other internal factors seem to acquire an influence on display performance. Instead of by emancipation of the original causal factors, the change in organization of display seems to be best explained by an *extension* of causal factors in the control of display behaviour (Fig. 13d). This explanation could also account for contradictary results, found in the literature (see introduction) about the relationship of displays with attack and escape behaviour. The establishment of such a relation bears heavily on the context in which the displays are observed.

4.4. Ritualization and ontogeny.

Since evolution depends on the modification of already existing mechanisms, phylogeny must be interpreted as modified ontogeny (DE BEER, 1940). Therefore it should be expected that changes in behaviour occurring in ontogeny are related to changes which have occurred in evolution. This seems indeed the case for the development of display behaviour in the black-headed gull. During ontogeny, the agonistic gull displays develop from intention movements of aggression and fear, and become more conspicuous. In ethology, it is widely accepted that several social displays have evolved similarly in the course of evolution from intention movements of *e.g.* locomotion, aggressive and fear behaviour. In the course of evolution, these movements are thought to become ritualized and closely related species each acquired their own species-specific displays (DAANJE, 1951; MORRIS, 1957; TINBERGEN, 1959; HINDE, 1969; BAERENDS, 1975). Indeed, the form of many incomplete forms of display, typical for young black-headed gulls, can be recognised in adult display of other gull species. For example, the bill-down oblique-like posture of young black-headed gulls is the normal adult oblique posture in the Hartlaubs gull (*Hydrocoloeus novae-holandiae hartlaubi*) (MOYNIHAN, 1955). The squat display in common gulls (*Larus canus*) (WEIDMAN, 1955) looks very similar to incomplete choking of young black-headed gulls. Herring gulls (*Larus argentatus*) perform no complete forward display but only incomplete ones, similar to young black-headed gulls (pers. observations). Furthermore, in contrast to adult display, the behaviour of young gulls of herring, common, little (*Larus minutus*), and black-headed gulls is rather similar to each other.

4.5. Functional aspects of the motivational development.

The behaviour of young animals should not merely be considered as incomplete and imperfect adult behaviour, but also as an adaptation to the specific needs of the young (OPPENHEIM, 1981; STAMPS, 1978). I would like to suggest several functional aspects of the changes occurring in the development of agonistic behaviour of black-headed gulls.

In young chicks, hiding was frequently performed when an intruder enters the territory. This is probably the best thing to do for young chicks, vulnerable as they are in a threatening situation. This hiding behaviour disappeared at the time the young are able to fly, (often the most effective escape strategy) and become too large to hide effectively. Withdrawal or escape as fear behaviour developed somewhat later than hiding, at the time the young were able to run and to find their way back to the nest.

Aggression developed at the end of the first week of life. Younger chicks are not able to recognize their parents and siblings (VAN RHIJN & GROOTHUIS, 1985). This results in the risk of misdirected aggression if this behaviour starts earlier. The frequency of aggression was at its peak during the period in which the young had to defend the territory on their own. When the young were older than 2-3 weeks of age, the parents were often not present on the territory, spending most of their time searching food for the young. By this time, the pumping display also became more pronounced in form, while bill-pecking started off from forward-like postures, with respect to form the opposite of aggressive pecks. This seems functional, because these larger and often hungry young have to develop a strong signal to convince their parents that they are not aggressive and to persuade them to give food. Aggression decreased, also in birds raised in the laboratory, at the age of 6 weeks, by the time the young were able to fly. In the field, young of this age are able to search food for themselves; they leave the colony, move around in flocks, and do not defend territories anymore.

Young gulls of several weeks old are likely to be weaker than adults. However, in the majority of aggressive interactions, young gulls were able to defend their territory effectively against adult intruders (personal observations). This was possible due to their tactics during such interactions, which deviated from that of adult gulls. When an intruder was approaching the territory, young gulls often hid in the vegetation until the intruder came too close. Then, they suddenly jumped on their feet, ran to the opponent, pecked aggressively and suddenly ran away to hide again. Intruders seemed to be quite surprised by these sudden attack and escape patterns. The young seem to be too vulnerable to give pronounced, long lasting display in front of the stronger opponent, by which they might also give away information on how likely the opponent is to be attacked.

Summary

In a study of the form development of the species-specific displays in the black-headed gull, a gradual change of these motor patterns was found, as well as a retardation of this change, in birds raised in a situation lacking the normal social context (GROOTHUIS, 1989). In this experimental context, low frequencies of aggressive and fear behaviour were also found. These results have led to the hypothesis that the ontogenetic change of display behaviour is influenced by the development of internal factors for agonistic behaviour. To put this idea to a test, a study was started to investigate the relation between the development of aggressive and fear behaviour and of display behaviour during ontogeny.

Standard stimulus experiments, simulating an adult intruder on the territory, were carried out at least once a week during the first 9 weeks of age in groups of territorial, hand-raised birds. The frequencies of two forms of fear behaviour, hiding and escape, and of aggressive pecking gradually increased in this order. The proportion of aggressive behaviour that was immediately followed by withdrawal was high in 2-week old chicks, but decreased considerably with age. The frequency of sudden stops after approach and of incomplete aggressive pecks increased with age, suggesting that overt aggression

became more inhibited by fear, resulting in longer lasting interactions with more display behaviour. This interpretation is supported by the finding that stopping as well as sitting occurred in the behavioral chain at the switch between overt aggression and overt escape.

The displays gradually changed in frequency and in form, via incomplete ones to the adult complete form. Oblique-, forward- and choking-like postures were almost exclusively performed in an agonistic context, in contrast to the begging display. It is concluded that each of these three agonistic displays develop from postures, dominated by a tendency to escape or to hide, to complete display by an addition of a simultaneously activated tendency to behave aggressively. This is based on:

1. similarities in frequency changes during ontogeny of overt aggressive and fear behaviour on the one hand, and the displays on the other hand;
2. the occurrence of the different displays during sudden stops after aggressive approach, during withdrawal, and in sitting which followed escape and was often followed by aggression;
3. the temporal relationship of the displays with overt aggression and with each other, and differences in this respect between incomplete and complete display;
4. similarity in form of the displays with overt aggressive and fear behaviour.

Functional aspects of this development are discussed.

The motivation of display in older gulls is studied separately, mainly by analysing normal social interactions. The increase in display frequency and decrease in overt aggression and fear during early ontogeny was maintained in later ontogeny. As a consequence, adults hardly showed overt aggressive behaviour. This finding could be explained by assuming an increasing mutual inhibition of each other's overt expression by internal mechanisms controling aggression and fear. However, this explanation could not account for other findings:

1. in contrast to young birds, adults frequently perform display outside agonistic contexts;
2. in contrast to young, adult birds no longer perform their display during those categories of locomotion for which evidence was obtained that they were caused by a simultaneous activation of aggression and fear;
3. adult gulls perform the oblique-forward sequence simultaneously with those of the opponent. The increase in synchronously performed display during late ontogeny suggests an increasing independence of display of the precise motivational state of the animal.

It is concluded that the displays, once developed under the influence of internal factors controlling aggressive and fear behaviour, become fixed in form and independent of these factors. It seems as if adult birds may use these motor patterns as a kind of subroutines, applicable in different behavioural programs.

If aggression is performed by adults, display is almost always performed also, suggesting that internal factors for agonistic behaviour, when aroused, still control display behaviour. It is suggested therefore that the ontogenetic change in causal organisation of display behaviour in gulls is more adequately described by the term "extension" of motivational factors than by the term "emancipation" of the original ones.

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Zusammenfassung

In einer vorangehenden Studie der Formentwicklung von artspezifischen Imponierhandlungen der Lachmöwe (GROOTHUIS, 1989) hatte sich gezeigt dass sich diese Verhaltensformen mit der Entwicklungszeit allmählich ändern, und der Lauf dieser Aenderungen verzögert wird bei Kücken, die normale soziale Auseinandersetzungen, in denen agonistisches Verhalten häufig vorkommt, haben entbehren müssen. Es schien daher möglich, dass sich Änderungen im Imponiergehaben während der Ontogenie — wenigstens teilweise — aus der Entwicklung der dem agonistischen Verhalten zugrunde liegenden Faktoren erklären liessen. Deshalb wurde in der jetzigen Arbeit untersucht in wieweit die Entwicklung von Aggression und Flucht mit jener der Imponierhandlungen zusammenhängt.

Während der ersten 9 Lebenswochen wurden bei handaufgezogenen Kücken, wenigstens einmal pro Woche, standardisierte Reizversuche durchgeführt, in denen das Ein-